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ADULT MOVEMENT AND LARVAL DISPERSAL OF *ARGYROZONA ARGYROZONA* (PISCES: SPARIDAE) FROM A TEMPERATE MARINE PROTECTED AREA

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Adult emigration and larval dispersal of carpenter *Argyrozona argyrozona* from the Tsitsikamma National Park (TNP), South Africa, were investigated using mark-recapture data and Acoustic Doppler Current Profiler measurements of currents. Tagging data showed that adult carpenter were mainly resident, with a small proportion (7%) leaving the TNP in both easterly and westerly directions. There was no relationship between fish movement patterns and fish size or time-at-liberty. Current patterns suggest that eggs and larvae spawned within the TNP are mainly transported eastwards towards established nursery grounds; the median estimated distance moved was 299 km (range 42–561 km) in 30 days (time to flexion). Given this pattern of ichthyoplankton dispersal, together with the fact that adult carpenter within the TNP displayed a high degree of residency and that they are much more abundant than in adjacent fishing grounds (catch per unit effort being 23 times greater), it appears that the TNP protects a viable carpenter spawner population capable of seeding adjacent fishing grounds.

Key words: currents, dispersal, eggs, larvae, mark recapture, movement patterns, Sparidae, transport

Carpenter *Argyrozona argyrozona* are an important component of the South African commercial linefishery (Brouwer and Buxton 2002). However, like many other reef fish, its catch per unit effort (*cpue*) has declined markedly since the early 1900s (Griffiths 2000). It is slow-growing and long-lived, with two distinct areas of abundance, one over the central Agulhas Bank and the other over the eastern Bank (Griffiths and Wilke 2002). Tagging studies suggest that exchange between these two populations is limited (Griffiths and Wilke 2002).

Given the limitations of conventional management tools such as bag and size limits, marine protected areas (MPAs) have been advocated as an effective strategy for the conservation of reef fish (Bohnsack 1998). Of central importance to this hypothesis is the ability of MPAs to supply recruits to adjacent fishing areas in sufficient numbers to maintain catches at predetermined levels (Carr and Reed 1993). In theory, MPAs benefit adjacent fisheries through both adult movement and larval seeding. However, supportive empirical evidence remains sparse. Because most no-take MPAs that protect reef fish are small, populations are impacted by fishing through edge effects, whereby fish move across reserve boundaries (Griffiths and Wilke 2002). Also, most MPAs are relatively new and the fish populations have not as yet recovered to pristine levels of abundance (Bohnsack 1998). By constrast, the Tsitsikamma National Park (TNP) on the south-east coast of South Africa is a well established (for nearly 40 years), no-take MPA that covers a relatively long coastline of approximately 75 km. It is the only MPA in South Africa that is perceived to be large enough (i.e. >50 km) to effectively provide complete protection for warm temperate sparids in the region (Griffiths and Wilke 2002).

The objective of this study was to establish whether the TNP seeds adjacent fisheries with adult and/or larval carpenter.

MATERIAL AND METHODS

The Tsitsikamma National Park extends between the Groot River (East; 30°04´S, 24°12´E) and the Groot River (West; 33°59´S, 23°34´E; Fig. 1). It extends 5.6 km offshore with reefs ranging in depth from shallow to c. 100 m (Tilney *et al.* 1996). This habitat and depth range is ideally suited to carpenter (Smith and Heemstra 1986, Smale and Badenhorst 1991).

Carpenter were caught from a skiboat using handline over a prominent reef (Middlebank; 34°02.72´S, 23°52.51´E), situated one mile from the coast and in

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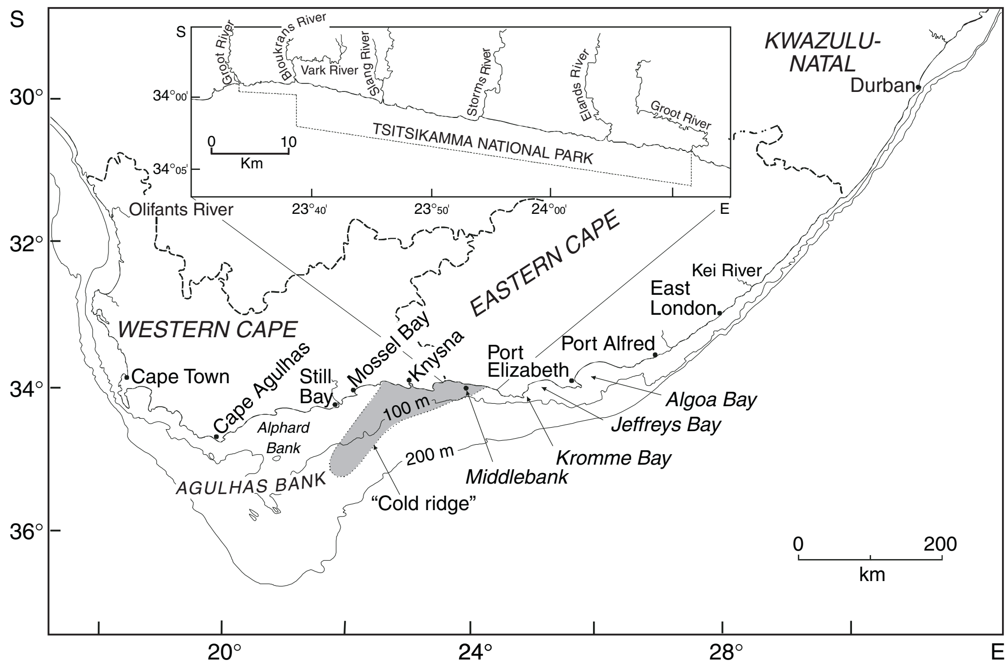

Fig. 1: Map of the study area, showing the position of the Tsitsikamma National Park on the south-east coast of South Africa and the locations mentioned in the text

36 m of water, near the centre of the TNP (Fig. 1). Fish were measured (mm, *FL*) and tagged on the left side with a dart D-tag (Hallprint, Australia), and when necessary the gas bladder was deflated using a hypodermic needle. Tags were individually coded and marked with a return address to the Oceanographic Research Institute (ORI), Durban. Number of fishers, fishing time, depth and location were recorded for each fishing trip. Recaptures within the TNP were made during scientific fishing operations between January 1997 and December 2000, whereas fish caught outside the park were reported to ORI by commercial and recreational fishers.

Fish were sacrificed during the spawning season and their ovaries preserved for histological analysis in order to identify spawning events, based on the presence of early (0–6 h) post-ovulatory follicles. To determine the fate of eggs and larvae spawned there, currents were measured using a 300 kHz Acoustic Doppler Current Profiler (ADCP). The instrument was deployed on Middlebank, an established spawning site for carpenter, between July 1998 and December 2002. Current direction and speed (cm s^{-1}) were recorded every 30 minutes at 2 m depth intervals between 3 and 31 m.

To establish likely settlement areas for carpenter larvae spawned on Middlebank, passive egg and larval drift were inferred using progressive vector plots calculated for 30 days after an established spawning event. Because carpenter eggs are buoyant (Davis and Buxton 1996) and generally found near the surface (Wood 1998), movement within the upper 11 m was used in this analysis. Spawning times were back-calculated according to the presence of early post-ovulatory follicles in histological ovary sections from fish collected on Middlebank. Histological analysis of capture-spawned carpenter revealed that early post-ovulatory follicles were present for up to 6 hours after a spawning event.

Spatial patterns in the distribution of juvenile carpenter were determined using data collected from research demersal biomass surveys carried out by Marine

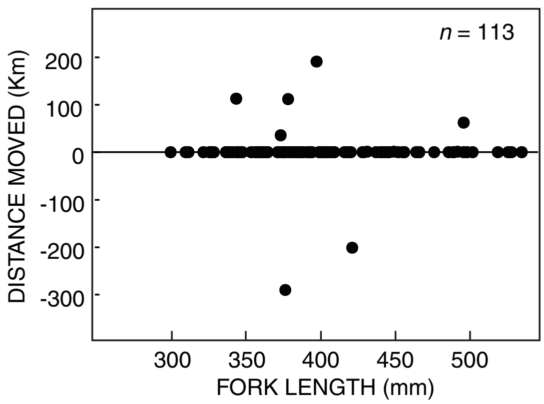

Fig. 2: Distance moved by different sizes of *A. argyrozona* tagged and released in the Tsitsikamma National Park. Positive indicates movement to the east and negative movement to the west

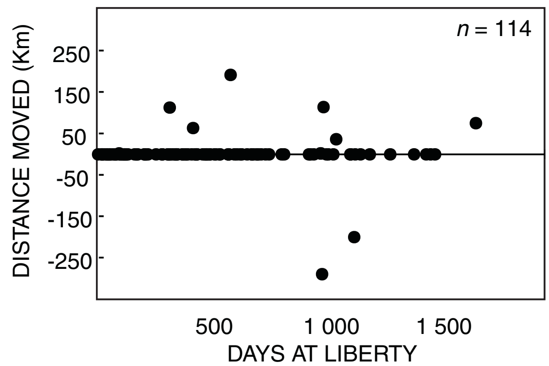

Fig. 3: Distance moved by tagged *A. argyrozona* relative to their time at liberty in the Tsitsikamma National Park. Positive indicates movement to the east and negative movement to the west

& Coastal Management between 1986 and 2001, using the swept area method (detailed in Badenhorst and Smale 1991). These data were converted to geo-referenced catch per unit effort (*cpue*; number of fish trawl^{-1} minute^{-1}) estimates. Distribution maps of *cpue* were obtained by means of Kriging (SURFER®; Golden Software, Inc., USA).

RESULTS

In all, 2 338 carpenter were tagged. Of these, 114 (5%) were recaptured, all larger than the size-at-50% (L_{50}) maturity. The average time at liberty for these fish was 526 days (range 9–1 691). Carpenter were largely resident, 90.3% being recaptured at the site of release; 2.7% were recaptured within the TNP away from the point of release, and 7.1% were caught outside the reserve. The eight fish recaptured outside the reserve travelled distances of between 36 and 290 km, in an easterly (75%) and westerly (25%) direction (Fig. 2). There was no evidence to suggest that fish at liberty for longer periods moved greater distances longshore (Fig. 3), but carpenter seemed to move into deeper water with increasing time at liberty (Fig. 4). Catch rate was on average 5.39 fish person^{-1} hour^{-1}.

Data from the demersal biomass surveys revealed two areas of abundance of juvenile carpenter. Smallest fish (50–100 mm *TL*) dominated over the eastern Agulhas Bank between Jeffreys Bay and Algoa Bay, and east of Cape Agulhas near the Alphard Banks (Fig. 5a). Larger fish (101–200 mm *TL*) concentrated inshore between Algoa Bay and Plettenberg Bay, and just east Cape Agulhas (Fig. 5b).

During the study period, currents moved in different directions and at varying velocities, depending on depth (Table I). The median distance moved by the

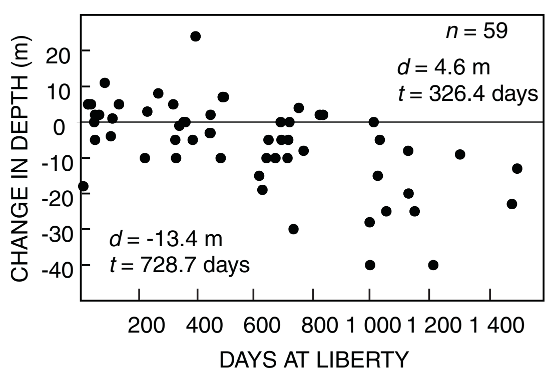

Fig. 4: Change in depth between the area at release and recapture for *A. argyrozona* tagged and released in the Tsitsikamma National Park. The mean change in depth (*d*) and time at liberty (*t*) for fish above and below the zero line are given. Negative values indicate movement into deeper water

Table I: Potential transport of larvae at four depths, for six consecutive months. Trajectories were calculated for 30 days using data collected by an ADCP moored at Middlebank in the Tsitsikamma National Park

Date of spawning	Depth (m)	Longshore movement (km)	On/offshore movement (km)	Net direction (degrees)	Compass direction
15 October 1998	5	352	8	94	ESE
	11	352	30	110	SE
	21	408	12	97	ESE
	31	248	23	70	NE
23 November 1998	5	360	23	75	NE
	11	352	12	97	ESE
	21	248	4	86	ENE
	31	16	10	35	NE
14 December 1998	5	583	38	70	NE
	11	561	12	86	ENE
	21	446	36	73	NE
	31	104	36	65	NE
14 January 1999	5	114	10	105	ESE
	11	144	18	110	SE
	21	90	22	125	SE
	31	59	3	276	WNW
16 February 1999	5	233	12	108	ESE
	11	245	10	96	ESE
	21	114	4	84	ENE
	31	6	14	23	NNE
15 March 1999	5	44	36	128	SE
	11	42	63	212	SW
	21	234	108	247	SW
	31	189	60	253	SW

surface layer (0–11m) during the 30-day period, following six spawning events, was 299 km eastwards (range 42–583 km). Progressive vectors for these six periods are shown in Figure 6, which shows that larvae were potentially transported eastwards and parallel to the 100 m isobath (Fig. 7).

DISCUSSION

Adult carpenter are clearly resident within the TNP, with only a small proportion of the population moving out of the reserve. This pattern is similar to that described for carpenter on the central Agulhas Bank (Griffiths and Wilke 2002), where most fish are resident and few are migratory. No attempt was made in the present study to quantify the potential number of individuals exported from the TNP, because of the limitation rendered by an under-reporting rate of 60% of recaptured tagged fish in the South African commercial linefishery (Brouwer 1997), as well as the effort differential (about 500 vessels in the fishing fleet in adjacent areas and one research vessel in the TNP). However, given the effort differential and the fact that only 7% of recaptures were made outside the TNP, adult emigration is expected to be low. The concept of a resident adult population within the TNP is further supported by an average *cpue* that was 23-fold higher than that recorded on the adjacent fishing grounds (Brouwer and Buxton 2002).

Griffiths and Wilke (2002) state that carpenter on the central Agulhas Bank move into deeper water as they grow. This also seems to be the case in the TNP, where depth of recapture increased with time at liberty. However, the movements recorded in this study took place on the same reef system, over horizontal distances of 20–2 000 m. No depth data were recorded for fish caught outside the TNP.

Currents remain the major determinant of pelagic larval dispersal (Lies and Goldman 1983), but larval behaviour is often more complex than have been described in the literature (Stobutzski 2001). Postflexion larvae of some teleosts can swim and orientate themselves towards physical cues in the current, thereby controlling their dispersal (Richards and Lindeman 1987, Lies 1991). Therefore, only dispersal of preflexion larvae was considered here. Carpenter are pe-

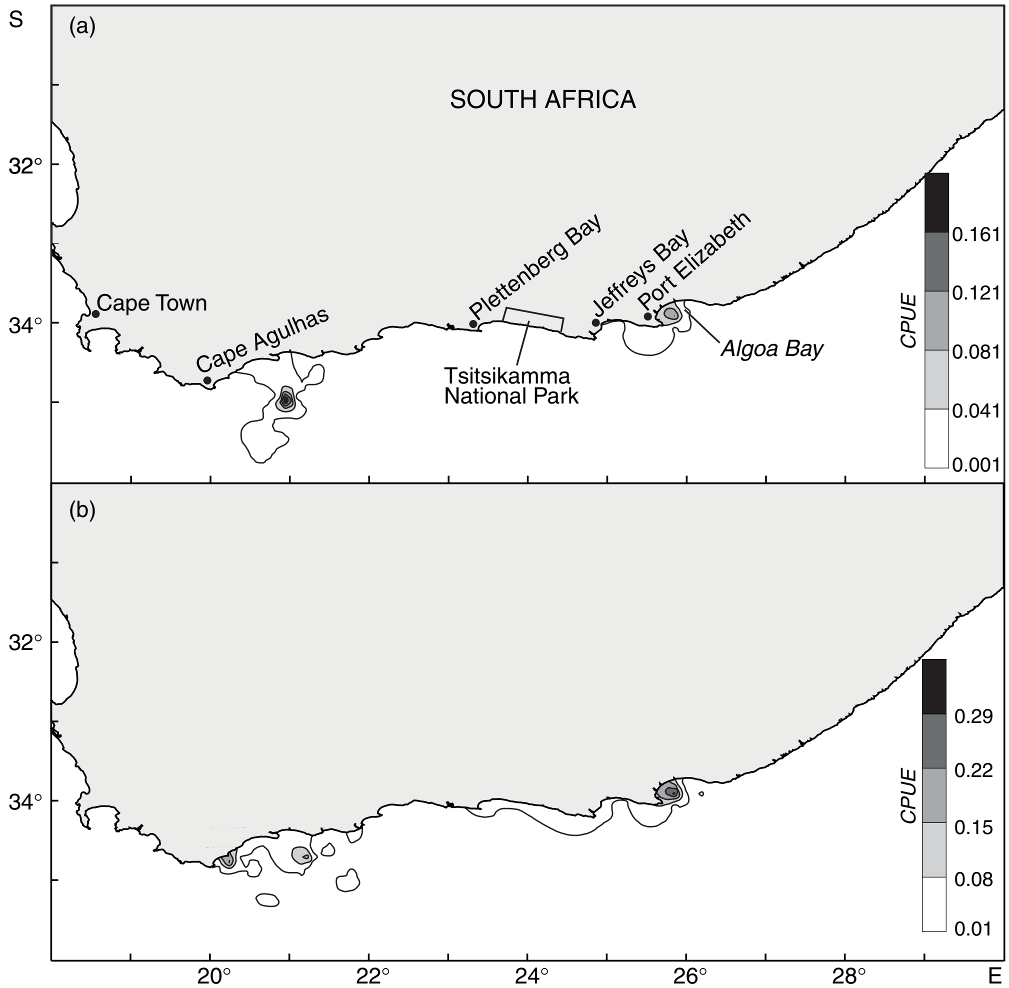

Fig. 5: Distribution of *A. argyrozona* at (a) 50–100 mm *TL* and (b) 101–200 mm *TL*, based on *cpue* (number of fish trawl^{-1} minute^{-1}), derived from 3 725 demersal trawls made during research cruises between 1986 and 2001

lagic spawners and their eggs float close to the water surface. Experimentally, it has been estimated that eggs of carpenter hatch after 26–30 h at 19°C, and that larvae undergo flexion after approximately 24 days (Davis and Buxton 1996). Eggs and preflexion larvae of carpenter are mainly in the upper 12 m in the TNP (Wood 1998).

Several attempts have been made to assess larval export of teleosts and chokka squid *Loligo vulgaris reynaudii* paralarvae from the TNP by studying current patterns. Tilney *et al*. (1996) used a bottom-moored (at 40 m deep) electromagnetic current meter and Attwood *et al*. (2002) tracked surface currents using short-period (6–24h) drogue releases. The present

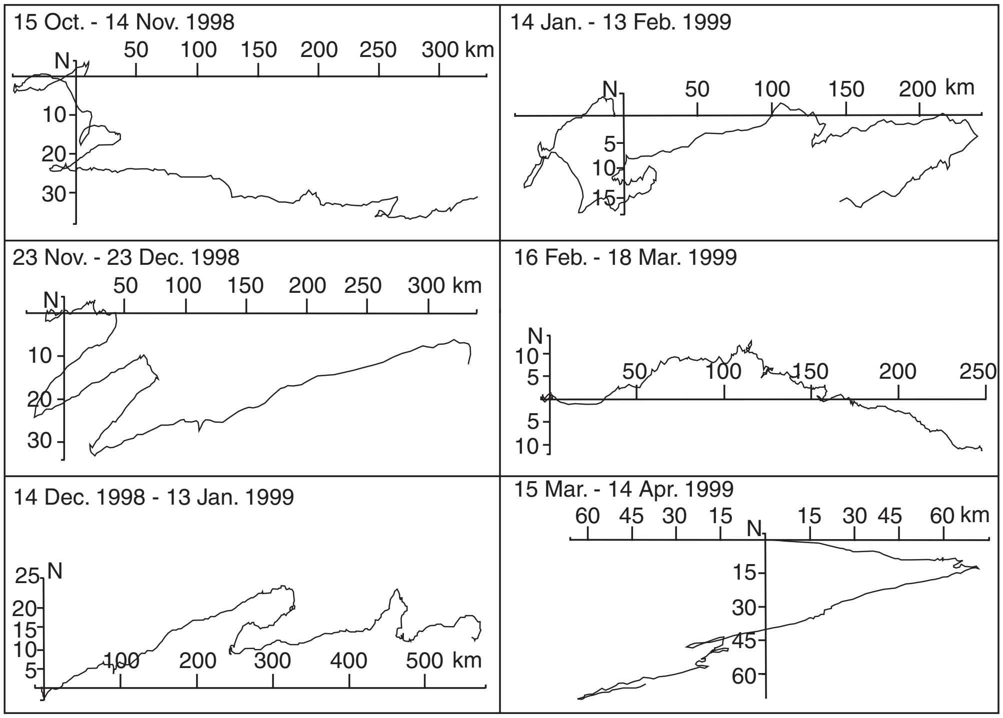

Fig. 6: Plots of six progressive vector tracks at 11 m deep, showing the potential trajectory of neutrally buoyant biological material from the Tsitsikamma National Park. The start of each track corresponds to a confirmed carpenter spawning event at the site of the ADCP

study used an ADCP that tracked currents continuously at discrete depths throughout the water column over a period of one year. Tilney and Buxton (1994) and Tilney *et al*. (1996) speculated that local inshore hydrography in the TNP could retain larvae in the reserve, but farther offshore, larvae could be transported up to 250 km westwards. However, Tilney *et al*. (1996) probably underestimated current speeds, because only bottom currents were considered in their study. Attwood *et al*. (2002), on the other hand, measured surface currents of short duration and suggested that dispersal was both east- and westward. Long-term current monitoring has nevertheless shown that the movement of the surface layer is mainly eastwards, with potential maximum distances exceeding 580 km in 30 days.

Unlike the above-mentioned previous studies, this study has linked water movement to observed spawning events, and both were measured simultaneously. The ADCP data indicated that the median distance moved by the surface water from the spawning location was 299 km east (range 42–583 km) in 30 days. The average current speed from this study (24 cm s^{-1}) suggests that larvae could be transported from the TNP to Algoa Bay within 30 days.

The spawner biomass surveys showed that small (50–100 mm *TL*) carpenter were most dense in the Algoa Bay region (Fig. 5), suggesting that the larvae settle and spend the first few months of their lives in this embayment. Larger juveniles (101–200 mm *TL*) were most abundant between Algoa Bay and Plettenberg Bay, indicating that they move westwards as they grow (Fig. 7). In support of this theory, Wallace *et al.* (1984), who conducted trawl surveys of the inshore bays between Mossel Bay and Algoa Bay, found juvenile carpenter (75–200 mm *TL*) only in Algoa Bay,

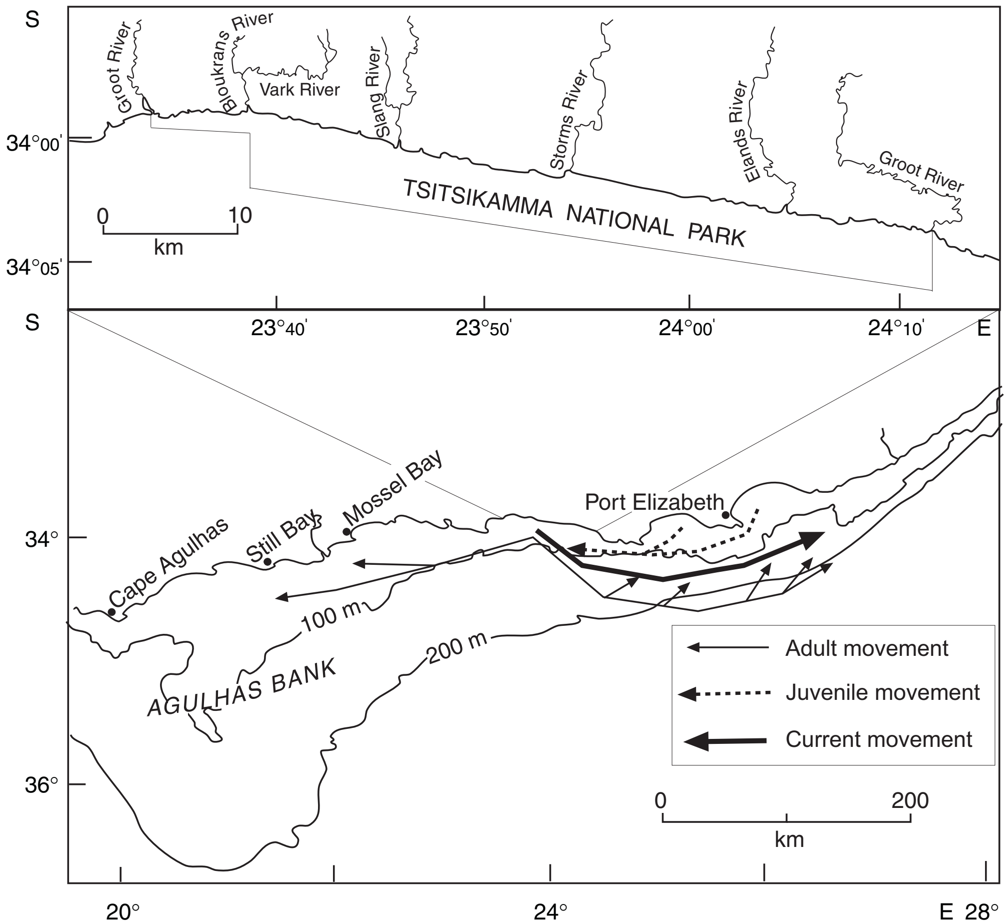

Fig. 7: A conceptual model showing current movements and direction over 30 days, and postulated movement of juvenile and adult *A. argyrozona* within and outside the Tsitsikamma National Park

Jeffrey's Bay and Plettenberg Bay. Semi-closed anti-cyclonic circulation patterns were found in Kromme Bay by Roberts and van den Berg (in prep.), who assumed them to be typical of other log-spiral shaped bays of the Eastern Cape (Roberts 1990), therefore theoretically retaining larvae.

Given that juvenile carpenter >200 mm *FL* were not found in the TNP and, assuming that juveniles disperse westwards as they grow, fish in the park probably recruit from the Algoa Bay nursery ground (Fig. 7). They are unlikely to originate from the more distant central Agulhas Bank nursery, because the "cold ridge" between Knysna and offshore of Still Bay (Fig. 1; Boyd and Shillington 1994) is believed to be a physical barrier to many warm, temperate demersal species (Griffiths 1997, Griffiths and Wilke 2002, Griffiths *et al*. 2002). Given the abundance of carpenter >250 mm *FL* off Port Alfred, the Algoa Bay nursery is also assumed to seed fishing grounds to the east.

It is likely that the TNP is an effective source of carpenter larvae. Its biomass within the reserve is probably dependent on recruitment of juveniles from nursery areas on the fishing grounds (Fig. 7). Spatially structured models are therefore necessary to gain a better understanding of the role of the TNP in enhancing stocks of important reef fish.

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